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Abstract

While the effect of weather on reproduction has been studied for many years in avian taxa, the rapid pace of climate change in arctic regions has added urgency to this question by changing the weather conditions species experience during breeding. Given this, it is important to understand how factors such as temperature, rain, snowfall, and wind affect reproduction both directly and indirectly (e.g. through their effects on food availability). In this study, we ask how weather factors and food availability influence daily survival rates of clutches in two arctic-breeding migratory songbirds: the Lapland longspur (Calcarius lapponicus), a circumpolar breeder, and Gambel's white-crowned sparrow (Zonotrichia leucophrys gambellii), which breeds in shrubby habitats across tundra, boreal and continental climates. To do this, we monitored clutch survival in these two species from egg-lay through fledge at field sites located near Toolik Field Station (North Slope, Alaska) across 5 years (2012-2016). Our results indicate that snowfall and cold temperatures decrease offspring survival rates in both species; although Lapland longspurs were more susceptible to snowfall. Food availability, quantified by pitfall sampling and sweep-net sampling methods, had minimal effects on offspring survival. Some climate models predict increased precipitation for the Arctic with global warming, and in the Toolik region, total snow accumulation may be increasing. Placed in this context, our results suggest that changes in snow storms with climate change could have substantial consequences for reproduction in migratory songbirds breeding in the North American Arctic.

Introduction

Global climate change is rapidly altering natural systems (Parmesan 2006) by disrupting seasonal patterns of temperature and precipitation (IPCC 2014) and increasing the occurrence of extreme events (Alexander et al. 2006; Mitchell et al. 2006; Tebaldi et al. 2006). To predict how climate change will affect populations, it is important to understand how demographic processes like offspring survival and recruitment into the breeding population are currently being affected. This requires understanding both how weather patterns are changing and how current temperature, precipitation, wind, and food availability affect reproduction.

The processes by which weather can affect reproduction are diverse including by altering seasonal timing (e.g., Boelman et al. 2017; Grabowski et al. 2013; Morton 1994; Norment 1992) and/or the number of offspring raised (e.g., Marrot et al. 2017; Martin and Wiebe 2004). In birds, the effects of precipitation, temperature, and wind on nestling survival have been documented in many observational studies (often conducted at temperate latitudes) and a few field experiments (summarized in Table 1). Offspring survival is often directly affected by events like nest flooding (Skagen & Adams 2012), hypothermia (Dawson et al. 2005), hyperthermia, and dehydration (Lombardo 1994; Cunningham et al. 2013). In general, rain or snow storms decrease nest survival while the effects of temperature and wind are much more varied across studies and depend upon the ecology of the species in question. For example, the ways that wind affects reproduction in aerial insectivores (e.g., Winkler et al. 2013) and seabirds (e.g., Weimerskirch et al. 2012) differ. Similarly, nestlings in northern and southern populations of the same species may face different fates in response to variation in weather (Table 1). Weather can also affect nest survival indirectly, by altering interactions of birds with their predators (Dickey et al. 2008; Lecomte et al. 2009) or with their food sources, for example, influencing food availability, foraging behavior, and offspring provisioning (Table 1). Therefore, understanding how changes in climate will affect a given species requires considering both direct and indirect effects of weather on nestling survival.

While the relationship between weather and nestling survival has been studied extensively in temperate regions, this relationship is less well understood in more remote arctic regions. There are numerous reasons why this relationship may be different in the Arctic than in other climates. First, predation rates are lower at high latitudes (McKinnon et al. 2010) and as a result weather may be one of the main factors influencing offspring survival. Second, the short growing season in the Arctic could restrict re-nesting (Martin and Wiebe 2004) and decrease the probability of weather-related nest-abandonment in arctic-breeders. Finally, the weather in the Arctic is extremely variable and offspring can be exposed to harsh environmental conditions throughout the incubation and nestling periods (Wingfield et al. 2004). Given that the Arctic is one of the fastest warming regions in the world (IPCC 2014), it is important to understand how current weather and changing weather patterns influence offspring survival in arctic-breeding species. Unfortunately, there are few baseline datasets exploring the relationship between weather and nestling survival in arctic species (McFarland et al. 2017) or longer term datasets that can evaluate how population numbers may be affected by climate change (Anctil et al. 2014; Dickey et al. 2008; Fossoy et al. 2015).

The goals of this study were to 1) identify the main drivers (i.e. temperature, rain, snowfall, wind, and/or food) of egg and nestling mortality in arctic-breeding birds and 2) assess whether reproductive response to arctic weather differs between a species that breeds exclusively in tundra habitats from that of a species with a climatologically diverse breeding range. In pursuing these goals, we aimed to contribute to the broader end of improving predictions of climate change impacts for arctic-breeding birds. To do so, we observed offspring of two species, the Gambel's white-crowned sparrow (*Zonotrichia leucophrys gambelii*) and the Lapland longspur (*Calcarius lapponicus*), from clutch initiation until fledging and looked for an association between daily offspring survival and short-term fluctuations in weather and food availability. While the Gambel's white-crowned sparrow is near the northern limit of its breeding range in the Arctic and breeds in a diverse range of shrubby habitats across northwestern regions of North America in tundra, boreal, and continental climates (Chilton 1995; Krause et al. 2015), the Lapland longspur breeds in a more restricted set of habitats, primarily in the Arctic, dominated by tussock and polygon tundra (Hussell 2002). Previous work in the system has

already shown that glucocorticoid levels (Krause et al. 2016b; Krause et al. 2016c), body condition (Krause et al. 2016c), clutch initiation (Boelman et al. 2017), and nestling growth (Pérez et al. 2016) are responsive to weather in these species.

We hypothesized that weather and food explain variation in nest survival and predicted that daily nest survival would decrease during periods of increased rain, recent snowfall, decreased temperature, and decreased food availability in both species, but that the extent of effects would differ between species. We hypothesized that tundra specialists are better adapted to breeding in arctic weather conditions than species with broad breeding distributions and predicted that egg and nestling survival rates in Lapland longspurs would be higher and less affected by unfavorable weather than those in Gambel's white-crowned sparrows.

Methods:

Study Species:

We studied Gambel's white-crowned sparrows and Lapland longspurs breeding at four sites in the vicinity of Toolik Field Station, North Slope Borough, Alaska, USA (Lat 68 °37' 39" N, Long 149° 35' 51" W). Gambel's white-crowned sparrows and Lapland longspurs are both small migratory passerines that travel thousands of kilometers to breed in northern regions. The Lapland longspur is a circumpolar breeder: in the Western Hemisphere it breeds in northern Canada, Greenland and across northern and western Alaska with isolated interior populations in more southerly tundra habitat (Hussell 2002). It overwinters in the mid-western United States and southern Canada (Hussell 2002). The Gambel's white-crowned sparrow occurs only in western North America, where it breeds in Alaska and Canada (though sometimes as far south as northern Washington State) and overwinters in California, Arizona, New Mexico, Texas and northern Mexico (Chilton 1995). Both species nest on the ground. Lapland longspurs nest in the sides of tussock-forming sedges, while Gambel's white-crowned sparrows nest at the base of shrubs (Boelman et al. 2015; Boelman et al. 2017; Chilton 1995). At our study sites, both species arrive on the breeding grounds in mid-May and quickly establish territories. Clutch initiation may continue from late-May to mid-June and nestlings typically hatch by mid-June (Boelman et al.

2017) and fledge 8-11 days later (Chilton 1995; Hussell 2002). Diet of nestling Lapland longspurs and Gambel's white-crowned sparrows at our sites includes crane flies *(Tipula cariniform)*, sawflies *(Tenthredinidae)*, midges *(Chironomidae)*, muscoid flies *(Muscidae)*, beetles *(Coleoptera)*, spiders *(Araneida)*, caterpillars *(Lepidoptera*), true bugs *(Hemiptera*) and other insects (Boelman et al. 2015). While the two species consume similar taxa, no analysis to date has compared the dietary composition of these two species and some differences may exist given that adults forage in slightly different habitats.

Site Description:

From 2012-2014, we collected data at four study sites (Roche Moutonnee, Toolik Field Station, Imnavait/ Kuparuk, and Sagavanirktok Department of Transportation) spanning 40 kilometers along the Dalton Highway on the North Slope of Alaska (Boelman et al. 2015). In 2015 and 2016, we collected data at Toolik Field Station, only. At each of the four sites, we established four 100 m transects, two in tussock tundra habitat (typical of Lapland longspur breeding sites) and two in shrub habitat (typical of Gambel's white-crowned sparrow breeding sites) to track arthropod phenology. We searched for nests on larger shrub and tussock tundra plot areas within 2 km of each transect (Roche Moutonnee, Toolik Field Station, Sagavanirktok Department of Transportation) and 3.5 km of each transect (Imnavait/ Kuparuk) (sampling methods described below).

Birds and Bird Nests:

At each site, we caught birds using mist nets and Potter traps and gave them numbered USGS metal leg bands and unique combinations of plastic color bands for individual identification. We found nests primarily by tracking focal females back to the nest or by flushing females from the nest. Males were also followed back to the nest while carrying food for nestlings. Our main goal was to find enough nests to estimate success and failure rates with appropriate statistical power. While we attempted to find all nests in the search area, it is possible that a few nests were not discovered. We monitored eggs in each nest by checking them on average every 2 days throughout incubation and until 9-12 days post-hatch. We considered nestlings successfully fledged if the nest was empty and intact

between 8 and 11 days post-hatch and parents were seen or heard close to the nest. We classified nest and egg failures using the following categories: un-hatched eggs (including failures due to lack of fertilization, incomplete development, or abandonment), depredated eggs and nestlings, nestlings found dead in the nest, and (rarely) eggs unintentionally broken by researchers. We classified clutches as depredated (instead of fledged) if nests were found empty prior to 7 days post-hatch (consistent with depredation by ravens *(Corvus corax)* and long-tailed jaegers *(Stercorarius longicaudus)*) or showed disruptions (disturbed nest lining or nest cup partially or fully torn out of the ground) typical of predation by Arctic ground squirrels *(Urocitellus parryii)*.

Weather:

Temperature, precipitation (rain and snow), and wind speed were measured hourly at each site, except at Imnavait where data were collected every half hour. Data at the Roche Moutonnee and the Sagavanirktok Department of Transportation were measured using the sensors described in Boelman et al. (2017). Data at Toolik were collected courtesy of the Toolik Field Station Environmental Data Center (Environmental Data Center Team, 2017) and data at Imnavait Creek were collected courtesy of long-term observations by the Arctic Observatory Network (Euskirchen et al. 2012). On rare occasions of weather sensor failure (2.6%-6.7% of hourly observations depending upon sensor type), values were interpolated or substituted with values from the nearest station.

Snowfall was monitored using time-lapse photography (Krause et al. 2016a). Camera data for Roche Moutonnee, Imnavait and select dates at Toolik were provided courtesy of the Toolik Field Station Environmental Data Center and for select dates at Toolik and Sagavanirtok Department of Transportation courtesy of the Deegan (Woods Hole Research Center, Woods Hole, MA) and Urban (University of Connecticut) laboratories. Cameras took images at the landscape scale at or near the nest search areas between 1 and 24 times per day. Given the variation in camera angles, spatial coverage, and sampling resolution across sites, they were only used to generate a binary response variable indicating whether snow had fallen over the previous 24-hour period centered on approximately noon. During one 15-day sampling gap at the Sagavanirktok Department of

Transportation in 2012, presence/ absence of snowfall was estimated using temperature and precipitation records (e.g. snow was scored as present if temperatures were below 0 °C and sensors registered precipitation).

Food availability:

Ground-dwelling arthropods were sampled weekly throughout the breeding season (clutch initiation to several weeks beyond fledging) at all transects using pitfall traps (Robel et al. 1995) using a monitoring scheme described in detail by Rich et al. (2013). Briefly, for pitfall traps, from late-May to late-July we placed clear plastic cups in the ground flush with the soil surface at 10 fixed locations along each 100-meter transect. Cups were filled approximately 2 cm deep with a 50-50 water-ethanol mixture to trap and preserve arthropods. Pitfall traps were deployed and active (cups filled with ethanol) for 48 hours at a time regardless of weather conditions. To estimate arthropod biomass, we dried and weighed all arthropods in each sample (2012; 2015-2016). In 2013 and 2014, we sorted each sample to family and used family-specific length-mass regression equations to obtain biomass estimates because we wanted to preserve specimens for museum curation (Pérez et al. 2016).

We also sampled shrub-dwelling and aerial insects weekly at all sites throughout the breeding season using the sweep-net monitoring scheme described in Boelman et al. (2015). For sweep-net samples, we used a standard insect net to collect 10 sets of sweep-net samples at both shrub and tussock tundra plots at each site every week from late May to late July. We dried and weighed all arthropods in each sweep-net sample to obtain a total biomass.

To estimate arthropod biomass outside of the sampling windows, we created predictive models of both pitfall and sweep-net biomass using methods detailed in Supplement 1. Briefly, we created Generalized Additive Models of arthropod biomass with linear parametric terms for weather (temperature, solar radiation, and precipitation) and a smooth (nonparametric term) for cumulative thawing degree days (TDD). We used TDD as our smooth predictor because it is a robust predictor of seasonal arthropod densities (i.e., arthropod phenology). Our predictive models explained a large

amount of variation in arthropod biomass for both pitfalls (adj. R^2 = 0.71) and sweep-nets (adj. R^2 = 0.41), which demonstrates their utility for generating biomass estimates on days when sampling was not conducted.

Statistical Analysis:

We tested the influence of temporal variation in arthropod biomass and weather on nest survival using a hierarchical logistic exposure model (Shaffer et al., 2004) modified for Bayesian approximation implemented in R 3.3.2 (R Core Team, 2016) and stan (Stan Development Team, 2016a) with package Rstan (Stan Development Team, 2016b). This approach was selected to account for temporal variation in when clutches were first found relative to clutch initiation date and allow us to determine whether time-specific changes in weather conditions affected nest survival rates. The unit of observation in our model is the survival of an egg (alive/dead) within a nest over an interval of time (t). Time is defined as the number of days between the current and previous observation (see Supplement 1 for details). The likelihood that an individual survives all t days is S^t, where S is the daily survival rate. Since survival can vary with age of the egg/nestling and clutch initiation date these factors were also included in the model. Additional details on clutch initiation date and nest age calculations appear in Supplement 1. Clutches were excluded if no eggs were laid (1 nest), if the fate of the egg could not be determined (2 nests), or if the nest was found failed and a date and age of failure could not be estimated (2 nests). We also excluded rare individual eggs that failed due to research activities (15 eggs). We restricted models to first clutches (209) excluding re-nests (30 nests)/ second broods (1 nest) because their fates are non-independent and because we expected that first broods and re-nests/ second broods may be affected differently by weather and food availability. A summary table of egg fates is provided in Table 2.

Weak prior probability distributions (priors) were assigned to all parameter values to ensure model fit. Fixed effects were assigned normal (mean= 0, SD=1) priors and the standard deviations of random effects were assigned half Cauchy (location= 0, scale= 1) priors. Final models were run with 3 chains for a minimum of 800 iterations and until rhat values (a model diagnostic with expected value equal to

1) for all parameters were below 1.1 and, with few exceptions below 1.02, to ensure model convergence. Chains were inspected visually for sufficient mixing to ensure that model results were appropriate. Model code is provided in Supplement 2.

First, to see what factors influenced daily survival in all birds, we fit a model with random intercepts for nest within year, species, site, and nest age (with a Gaussian process to allow for similarities in outcomes at similar nests) plus fixed effects for temperature, wind, precipitation, food, clutch initiation date, and all two and three-way interactions between temperature, rain, and sweep-net or pitfall biomass. Since food availability and weather parameters fluctuated on short time-spans, these factors were incorporated into the model as mean values corresponding to the interval between nest checks centered around noon. All continuous variables were centered. Snowfall was included in the model as the proportion of days between nest checks with new snow present. A random effect for each egg was not included because it was non-informative and interfered with model convergence. We built a second model specifically to test for species differences in survival and species differences in reproductive sensitivity to weather. This model included fixed effects for species and interactions between species and temperature, snowfall, precipitation, wind, food availability, and clutch initiation date. This model contained random effects for nest within year, site and nest age as before. Model results are reported as posterior distributions with mean (β) and 95% highest posterior density interval (HPDI) on a log-odds scale. We also used the R package "rethinking" (McElreath 2016) to test whether the probability of offspring depredation differed between species using a mixed model with a binomial distribution; random effects for year, nest, and site; and a fixed effect for species. Results are reported on a log-odds scale.

We also conducted a supplementary analysis to compare weather across years. This analysis was restricted to weather conditions between the 141st and 191st days of the year, which represented the maximum period of time from clutch initiation to fledge in first clutches. Hourly temperature and wind speed during the nesting period in each year were modeled using the "rethinking" package (McElreath 2016) with a Gaussian distribution and a random effect for site. Hourly precipitation presence (yes/ no)

and daily snowfall (yes/ no) were modeled using a binomial distribution and a random effect for site and results for binomial models are reported on a log-odds scale.

Results:

Overall 240 clutches with 1086 eggs observed over 5 years were included in the final analysis. Of these, 209 clutches (962 eggs) were first broods. Re-nests presented 30 clutches (116 eggs) and second broods 1 clutch of 3 eggs. Our sample included 108 nests (498 eggs) of Gambel's white-crowned sparrow clutches and 101 clutches (464 eggs) of Lapland longspur clutches. A detailed breakdown of the final fate of eggs by year and species is provided in Table 2. There was no difference in the probability of predation between species (β= 3.462, 95% [-4.636, 11.062]).

Weather conditions:

Weather conditions differed across the years. Hourly temperatures in 2014 were colder than all other years of the study (β= -2.801, 95% [-3.055, -2.549]). While 2016 (β= -1.542, 95% [-1.955, -1.094], Supplement 2) was warmer than 2014, it was colder than the other three years. The year 2016 (β= -0.307, 95% [-0.403, -0.207]) was also windier than all years, except for 2014, which featured similar hourly wind speeds (β= 0.032, 95% [-0.026, -0.089]). The hourly probability of rain was higher in 2013 (β= 0.392, 95% [0.258, 0.544]) and 2016 (β= 0.482, 95% [0.284, 0.687]) than all other years, but did not differ between the two. There was no difference in the absolute daily probability of snowfall across years. Despite the lack of a difference in daily probability of snowfall across the entire nesting season, the years 2015 and 2016 featured multiple late-season snow storms notable for their intensity and total snow accumulation. In both of these years, multiple snow storms occurred after the population had begun to nest. In 2016, these storms were dated May 25th, June 5th-6th, June 8th, June 10th, and June 21st and in 2015 they occurred on May 29th, 31st June 2nd and 11th.

Daily survival

In our first model, daily survival rates were influenced by snowfall and temperature between nest checks. Daily survival increased with temperature (β=0.101, 95% [0.016, 0.182], Supplement 3) and

there was a trend towards decreased survival with snowfall (β= -0.847, 95% [-1.767, 0.019], Supplement 3). The main effects of food availability quantified by pitfall and sweep-net sampling on daily survival rates were negligible; however, there were significant interactions between food availability and weather parameters. Daily survival rates increased slightly with pitfall biomass overall (β= 0.021, 95% [0.006, 0.037], Supplement 3; Fig. 2). However, there were two-way negative interactions between pitfall biomass and rain (β=-0.687, 95% [-1.227, -0.117], Supplement 3) and pitfall biomass and temperature (β= - 0.003, 95% [-0.005, -0.001], Supplement 3), such that at high average temperatures or in rainy conditions daily survival went down with increases in pitfall biomass. There was a trend for increased daily survival rates with high sweep-net biomass overall (β=0.036, 95% [-0.001, 0.073], Supplement 3), with a positive two-way interaction between sweep-net biomass and rain (β= 1.281, 95% [0.366, 2.238], Supplement 3) and a negative three-way interaction between sweep-net biomass, rain, and temperature (β= -0.496, 95% [-0.776, -0.232], Supplement 3). In rainy conditions, high sweep-net biomass had a stronger positive effect on daily survival than under dry conditions, however this depended upon temperature. When temperatures were low and it was rainy, increases in sweep-net biomass had strong positive effect on daily survival rates, however there was a decrease in survival rates with increasing sweep-net biomass when temperatures were high and it was rainy. The relationship between temperature and sweep-net biomass was reversed under dry conditions. Additionally, survival decreased with later clutch initiation dates (β=-0.372, 95% [-0.600, -0.131], Supplement 3). Posterior distributions for random effects showed that survival varied across years and was lowest in 2015 and 2016 (Supplement 3). Survival also varied with egg/ offspring age (Supplement 3).

In our second model comparing survival rates between species, daily survival rates in Lapland longspurs were lower than in Gambel's white-crowned sparrows (β=-1.226, 95% [-2.481, -0.020], Supplement 3, Fig. 1). Daily survival of Lapland longspur offspring decreased more than Gambel's white-crowned sparrow offspring with snowfall (β=-2.777, 95% [-4.178, -1.289], Fig. 2, Supplement 3) and increased less with higher temperatures (β=-0.228, 95% [-0.381, -0.089], Fig. 3. Supplement 3).

Increases in survival with pitfall biomass were stronger in Lapland longspur offspring than in Gambel's white-crowned sparrow offspring (β= 0.134, 95% [0.085, 0.188], Supplement 3).

Many of the main effects were consistent across the two survival models. In the species interaction model, there was also a positive main effect of temperature (β=0.340, 95% [0.231, 0.467], Supplement 3) and a negative main effect of clutch initiation date (β= -0.328, 95% [-0.608, -0.022], Supplement 3) on daily survival rates. Again, survival varied across years with the lowest survival rates in 2015 and 2016 (Fig 4, Supplement 3). The species interaction model also found variable survival across egg/ nestling ages.

Discussion:

Our results show that snowfall and low temperatures influence reproductive success in Lapland longspurs and Gambel's white-crowned sparrows. Lapland longspur offspring had lower survival rates overall and greater declines in survival with snowfall. Food availability by itself had minimal effect on survival but did modulate the effects of weather. Clutch initiation date also influenced survival rates, with early clutches exhibiting higher daily survival.

Our result that snowfall and cold temperatures influenced nestling survival was consistent with other studies (Table 1; Jehl 1970; Jehl and Hussell 1966). This is also consistent with our finding that the two years with the lowest nest survival rates (Fig. 4) were wetter than historical average climate during June (Alaska Climate Research Center and National Weather Service, 2017). Despite this consistency, the effect of snowfall on nestling mortality in arctic-breeding passerines was somewhat unexpected, given that previous work in another species, the Smith's longspur *(Calcarius pictus),* has suggested that at least some species may be relatively robust to such environmental challenges (McFarland et al. 2017). The precise timing of snowfall relative to nesting phenology may affect survival. For example, the June 21st 2016 storm killed many newly hatched nestlings that lacked the ability to thermoregulate (Chilton 1995), had minimal energetic reserves, and were likely difficult to provision during the storm. In contrast, a few clutches still incubating survived. Precipitation may also

have lasting negative sub-lethal effects by depressing growth rates of both Lapland longspur and Gambel's white-crowned sparrow nestlings (Pérez et al. 2016).

Our study also found that Lapland longspurs had lower survival rates than Gambel's white-crowned sparrows (Fig. 4), which was not due to differences in predation. Lower survival rates could be driven by a greater susceptibility of Lapland longspurs to snowfall (Fig 2). These results are contrary to our original prediction that a tundra habitat specialist (i.e., Lapland longspurs) would be more resistant to harsh weather than a species breeding at the northern edge of its range (i.e., Gambel's white-crowned sparrows). This could be due to numerous factors including differences in how the two species alter parental care in response to weather events, differences in how offspring of the two species tolerate adverse weather, or differences in the microclimates provided by tussock and shrub nesting sites including the response of food resources within those microhabitats to weather events. For example, temperatures taken with HOBO dataloggers at nest microhabitats in one year of the study suggest that minimum temperatures may be lower near Lapland longspur nests than near Gambel's white-crowned sparrow nests. The reproductive impact of nest losses during snowfall for Lapland longspurs is compounded by the low rate of Lapland longspur re-nesting. During the 5 years of our study we detected only 1 Lapland longspur re-nest (Table 3), despite the population at our site experiencing heavy nest mortality during snowfall. This is consistent with observations by Custer and Pitelka (1977) that second nests were rare in Lapland longspurs in Barrow, Alaska and is in contrast to the 30 Gambel's white-crowned sparrow re-nests observed during the same time period (Table 3). This suggests that the overall window for reproduction in Lapland longspurs may be more limited than in Gambel's white-crowned sparrows, potentially due to earlier onset of photorefractoriness. If this is the case, then first nest failures in Lapland longspurs may have a greater effect on total yearly reproductive output at individual and population levels.

These findings raise two important questions: will climate change in the Arctic increase frequency and intensity of late season snowstorms and could this mean that climate change will have more severe consequences for Lapland longspurs than Gambel's white-crowned sparrows? Historic precipitation

records for Alaska are sparse and climatological analyses on different spatial scales report divergent results (McAfee et al. 2014; McAfee et al. 2013). However, one source for the Toolik region suggests that snowfall may have increased over the last 30 years and that precipitation may increase in the future (Cherry et al. 2014). While spring snowmelt is advancing (Stone et al. 2002; Tape et al. 2016) in some Arctic locations, few datasets capture the pulse snow storms midsummer we describe here. One potential outcome of climate change is a pattern of earlier snowmelt, followed by late season storms. While warmer arctic spring temperatures may lead to earlier nesting (Grabowski et al. 2013; Liebezeit et al. 2014; McFarland et al. 2017), if this warming pattern is accompanied with an increased incidence in late season snow storms, reproductive failure may increase. Early nesting under warm conditions followed by nest failure during cold snaps and snowstorms has been observed in other species (Decker and Conway 2009; Whitehouse et al. 2013). A similar phenomenon has been observed in alpine plants which are emerging earlier with climate change but are being killed by the increasing frequency of late season frosts (Inouye 2008). However, without more robust precipitation predictions with greater temporal resolution for Northern Alaska, including late-season snowstorms, it is unclear whether this is a likely outcome of global warming.

The susceptibility of Lapland longspurs to snowfall raises the possibility that they may be particularly affected by global climate change relative to Gambel's white-crowned sparrows. Given that Lapland longspurs are projected to lose breeding habitat with future climate warming and shrub advancement on the tundra (Boelman et al. 2015), it is important to understand how other forms of vulnerability may exacerbate the challenges this species already faces. Conversely, Gambel's white-crowned sparrows are anticipated to gain breeding habitat in addition to the potentially more robust response to storms revealed in this study. Some studies suggest that climate change is affecting the diversity of avian communities and that habitat generalists are benefitting to the detriment of specialists (Davey et al. 2012; Davey et al. 2013; Le Viol et al. 2012). To the extent that Lapland longspurs are tussock and polygon tundra habitat specialists while Gambel's white-crowned sparrows breed in shrubs across polar, boreal, and continental climates, our findings may be consistent with this hypothesis. Sampling

across a wider portion of these species' breeding ranges could provide a more robust test of this hypothesis.

A final major finding from our study is that the effect size of food availability on survival rates was minor relative to other factors. There was no main effect of sweep-net biomass on daily survival rates and only a small positive effect of pitfall biomass. Food availability in the Arctic during summer is high overall and this could buffer individuals from the effects of climate change. Below a certain threshold, changes in food availability might have large effects on survival, but above that threshold the relationship between survival and food availability may be minimal. Tulp and Schekkerman (2008) found that while the timing of both peak arthropod biomass and biomass above the threshold for raising young have shifted earlier in Siberia, the total duration of time with sufficient biomass to provision offspring remained the same. Our models of predicted arthropod biomass indicate that food availability reaches high values for an extended period during the breeding season, continuing several weeks beyond fledging, with strong transient dips during periods of bad weather (Supplement 1). It seems likely, therefore, that the greatest effects of food on reproductive success in our system will be seen when reductions in food availability due to weather augment the effects of weather itself. The significant interactions between weather and food availability in our models support this explanation (Supplement 3).

Conclusions:

Our hypothesis that weather and food availability influence offspring survival was partially supported. This study suggests that snowfall and temperature are important factors influencing daily nest survival in two species of migratory arctic breeding songbirds, but that food availability has minimal effect. Contrary to expectation, we found that the Lapland longspur, a tundra habitat specialist, is more susceptible to snowfall than Gambel's white-crowned sparrow, which uses a broader range of breeding habitats. This suggests that effects of late-season snow storms, particularly at vulnerable life-history stages like nesting, deserve greater attention in climate change research.

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Figure Legends

Fig 1: Daily survival probabilities for Lapland longspur (LALO) and Gambel's white-crowned sparrow (GWCS) offspring given by the species interaction model. The thick black line in the box plots represents the average daily survival for each species across the entire nesting period, boxes represent the 25th and 75th percentile and whiskers represent 1.5 times the inter-quartile range. Posterior distributions reflect the influence of species on survival rates when all other values in the model are held constant.

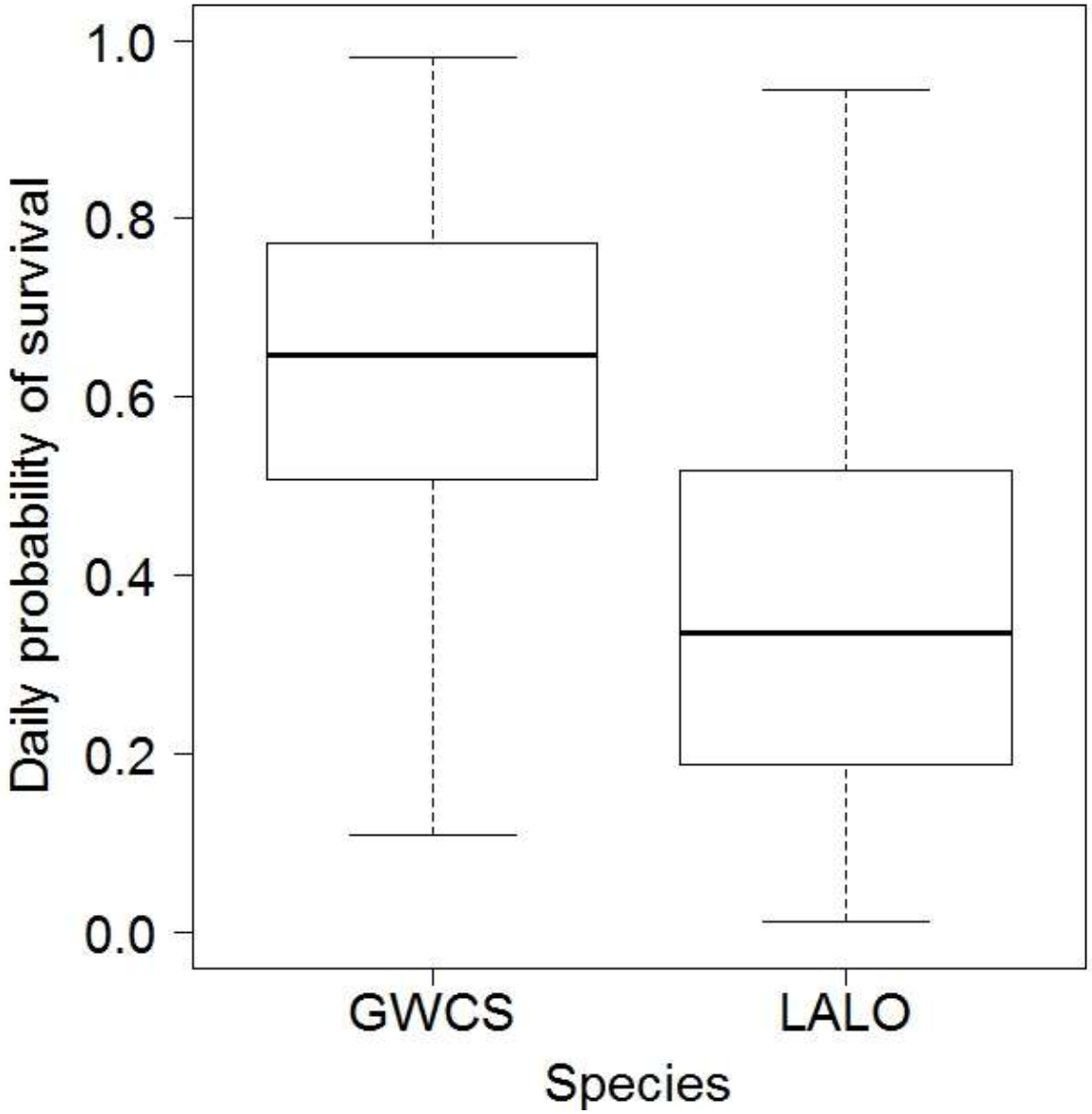
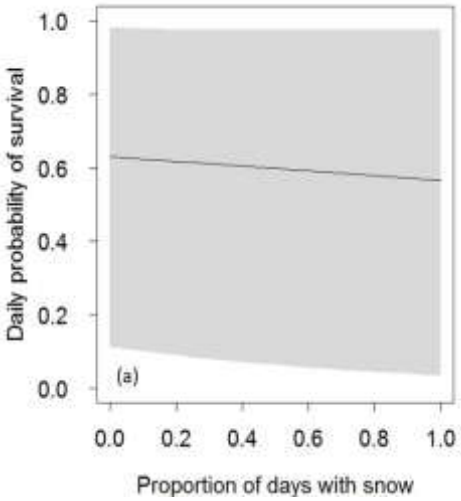


Fig 2: Daily survival probability of Gambel's white-crowned sparrow (a) and Lapland longspur (b) eggs and nestlings against proportion of days with snowfall between nest checks. For both panels, the thick black line represents model predictions sampled from the posterior for the average nest and the gray shaded region is the 95% HPDI. Posterior distributions are calculated with other model parameters held constant.



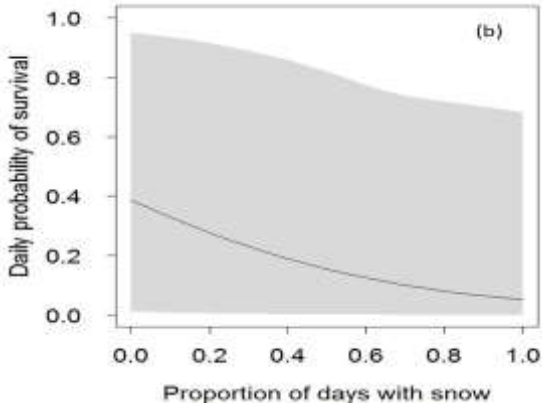


Fig 3: Daily survival probability of eggs and offspring for Gambel's white-crowned sparrows (a) and Lapland longspurs (b) with mean temperature. The black line represents predictions for the average nest sampled from the model posterior and the gray shaded region represents a 95% HPDI around those predicted values. Posterior distributions reflect the influence of average temperature on daily survival probability when all other model parameters are held constant.

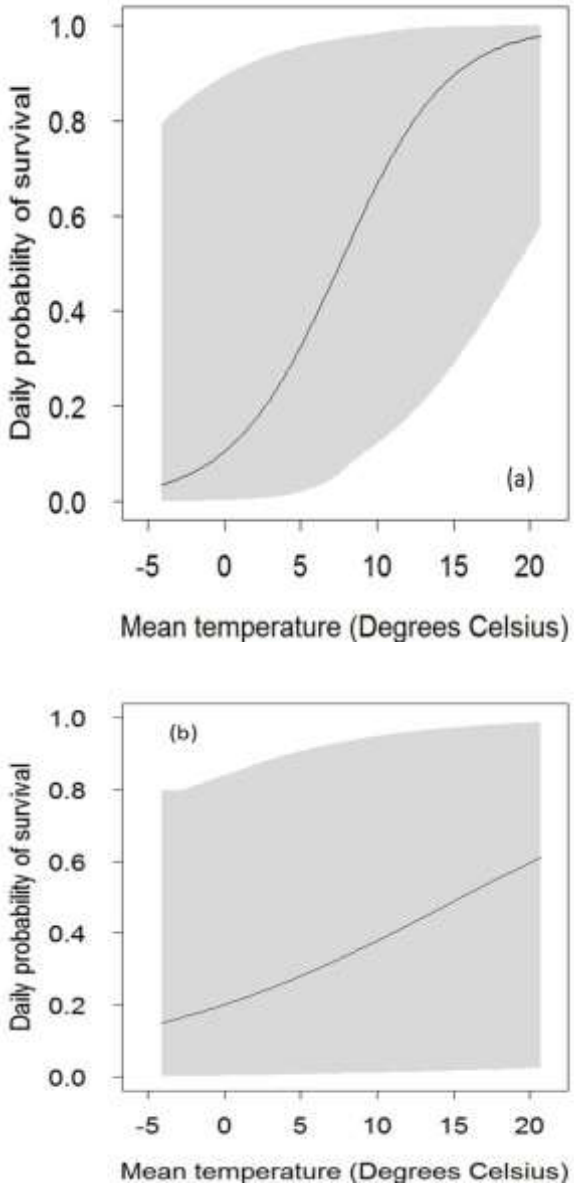


Fig 4: Random effect posterior distributions for variation in daily survival rates across nests within a year from species interaction model. For each box plot, the thick black line represents the mean of the coefficient posterior for each year, boxes represent the 25th and 75th percentile, and whiskers represent 1.5 times the inter-quartile range.

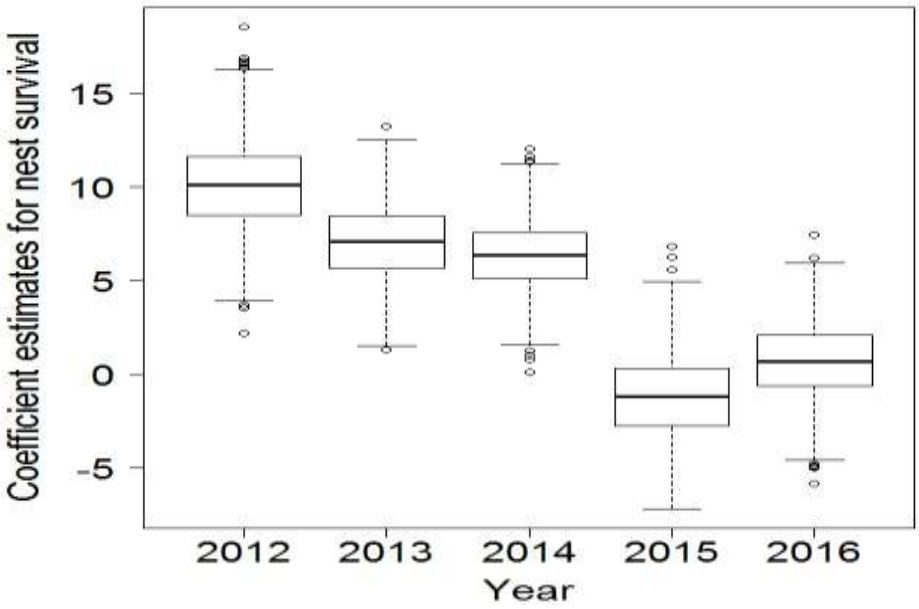


Table Legends

Table 1. Select studies documenting the relationship between weather and offspring survival. Under "effect", plus signs (+) indicate a positive effect of the weather parameter on offspring survival and minus signs (-) indicate a negative effect on survival.

Factor	Timescale	Effect	Species	Survival Metric	Food effect	Citation
Field Observations						
Rain	7 months	(+)	Brewer's sparrow *(Spizella breweri)*	Number of fledglings	N/A	(Rotenberry and Wiens 1991)
Rain	daily	(-)	Great tit *(Parus major)*	Likelihood of abandonment	N/A	(Bordjan and Tome 2014)
Rain	7-14 days	(-)	Northern wheatear *(Oenanthe oenanthe)*	Fledging success and recruitment	(-) (parental visitation)	(Oberg et al. 2015)
Rain	7-14 days	(-)	Pied flycatcher *(Ficedula hypoleuca)*	Hatching success and Fledging success	N/A	(Eeva et al. 2002)
Rain	1-4 days	(-)	Pied flycatcher *(Ficedula hypoleuca)*	Individual mortality rate	N/A	(Siikamaki 1996)
Rain	7 months	(+)	Sage sparrow *(Amphispiza belli)*	Number of fledglings	N/A	(Rotenberry and Wiens 1991)
Rain	22-26 days	(-)	Middle spotted woodpecker *(Dendrocopos medius)*	At least one success/ nest	N/A	(Pasinelli 2001)
Rain	daily	(-)	Wrynecks *(Jynx torquilla)*	Daily brood survival	None (parental visitation)	(Geiser et al. 2008)
Rain	5 days	(-)	Hoopoe *(Upupa epops)*	Number of fledglings	(-) (parental visitation, food mass)	(Arlettaz et al. 2010)

Rain	Months (multiple periods quantified)	(+)	Greater snow geese *(Chen caerulescens atlantica)*	Probability of at least 1 success/ nest	N/A	(Dickey et al. 2008)
Rain	49-50 days	(-)	American kestrel *(Falco sparverius)*	Probability of mortality	(-) (parental visitation, food mass)	(Dawson and Bortolotti 2000)
Rain	2 months	(-)	Peregrine falcon *(Falco peregrinus)*	Percent mortality	N/A	(Anctil et al. 2014)
Rain	5 months	(-)	Hen harrier (Spain) *(Circus cyaneus)*	Annual fledging success	N/A	(Garcia and Arroyo 2001)
Rain	5 days	(-)	Hoopoe *(Upupa epops)*	Number of fledglings	(-) (parental visitation, food mass)	(Arlettaz et al. 2010)
Rain	Daily	(-)	Lark bunting *(Calamospiza melanocorys)*	Nest success	N/A	(Skagen and Adams 2012)
Rain	Annual	(+)	Lark bunting *(Calamospiza melanocorys)*	Nest success	N/A	(Skagen and Adams 2012)
Snow	Single event	(-)	American pipits *(Anthus rubescens)*	Percent mortality	N/A	(Hendricks and Norment 1992)
Snow	Single event	(-)	Red-faced warbler *(Cardellina rubrifrons)*	Percent mortality	N/A	(Decker and Conway 2009)
Snow	Single event	(-)	White-tailed ptarmigan *(Lagopus leucurus)*	Nest success	N/A	(Martin 2006)
Snow	Multiple events modeled on multiple time lags	(-)	Antarctic petrels *(Thalassoica Antarctica)*	Daily survival	N/A	(Descamps et al. 2015)
Storm	Single events	(-)	Horned larks (*Eremophila alpestris*)	Daily survival	N/A	Martin et al. 2017
Storm	Single events	(-)	Savannah sparrows (*Passerculus sandwichensis*)	Daily survival	N/A	Martin et al. 2017
Temp	Days-weeks	None	House sparrows *(Passer domesticus)*	Fledging success	N/A	(Pipoly et al. 2013)
Temp	Annual	(+)	Lark Bunting *(Calamospiza melanocorys)*	Nest success	N/A	(Skagen and Adams 2012)
Temp	7-14	(+)	Pied flycatcher	Hatchin	N/A	(Eeva et al. 2002)

	days		*(Ficedula hypoleuca)*	g and fledging success		
Temp	2 months	None	Snow bunting *(Plectrophenax nivalis)*	Number of fledglings	N/A	(Fossoy et al. 2015)
Temp	daily	(-)	Wryneck *(Jynx torquilla)*	Daily brood survival	(inverted U) parental visitation	(Geiser et al. 2008)
Temp	5 days	(+)	Hoopoe *(Upupa epops)*	Number of fledglings	(+) (parental visitation, food mass)	(Arlettaz et al. 2010)
Temp	Months (multiple periods quantified)	(+ / -)	Greater snow geese *(Chen caerulescens atlantica)*	Probability of at least 1 success/ nest	N/A	(Dickey et al. 2008)
Temp	2 months	(+)	Hen harrier (Scotland) *(Circus cyaneus)*	Fledging success	(-) provisioning rate	(Redpath et al. 2002)
Temp	1 month	(-)	Hen harrier (Spain) *(Circus cyaneus)*	Hatching success	N/A	(Garcia and Arroyo 2001)
Temp (high)	daily	None	Brewer's sparrow *(Spizella breweri)*	Number of fledglings	N/A	(Rotenberry and Wiens 1991)
Temp (high)	1 month	(-)	Golden eagle *(Aquila chrysaetos)*	Brood success	(+) food abundance can interact with weather to compensate for hot weather negative effect.	(Steenhof et al. 1997)

Temp (high)	15-21 days	(-)	Kalahari Common fiscal *(Lanius collaris)*	Prolonged parental care decreases fledging success	(-) provisioning rate	(Cunningham et al. 2013)
Temp (high)	6-18 days	(+)	House sparrows *(Passer domesticus)*	Hatching success	N/A	(Pipoly et al. 2013)
Temp (high)	daily	(-)	Sage sparrow *(Amphispiza belli)*	Number of fledglings	N/A	(Rotenberry and Wiens 1991)
Temp (low)	6-18 days	(-)	House sparrows *(Passer domesticus)*	Hatching success	N/A	(Pipoly et al. 2013)
Temp (low)	1-3 days	(-)	Tree swallows *(Tachycineta bicolor)*	Daily survival rate	(-) abundance	(Winkler et al. 2013)
Temp (low)	22-26 days	(-)	Middle spotted woodpecker *(Dendrocopos medius)*	Probability of at least 1 success/ nest	N/A	(Pasinelli 2001)
Wind	1 month	(-)	Barn swallows *(Hirundo rustica)*	Percent fledged	(-) abundance	(Moller 2013)
Wind	2 months	(+)	Wandering albatross *(Diomedea exularis)*	Breeding success	(-) parental foraging trip duration	(Weimerskirch et al. 2012)
Field Experiments						
Rain	25 days	(-)	Peregrine falcons *(Falco peregrinus)*	Nestling survival rate	N/A	(Anctil et al. 2014)
Temp	12 days	(+)	Tree swallows *(Tachycineta bicolor)*	Proportion fledged	N/A	(Dawson et al. 2005)

Table 2: A summary identifying the number of eggs and nests from first broods observed each field season at Imnavait (IMVT), Roche Moutonnee (ROMO), Sagavanirktok Department of Transportation (SDOT), and Toolik (TLFS) field sites and the final fates of each. Un-hatched eggs include those that did not hatch due to lack of fertilization, unknown developmental defect, or abandonment. Depredated eggs include eggs or nestlings that were consumed (some eggs in this category may not have been fertilized). Non-predation deaths include all nestlings than died due to a factor other than predation (e.g. abandonment, illness, injury, hypothermia).

Gambel's white-crowned sparrow							
Year	**Sites**	**Total**		**Un-hatched**	**Depredated**	**Non-predation death**	**Fledged**
		eggs	nests	eggs	eggs/ nestlings	nestlings	nestlings
2012	IMVT, ROMO, SDOT, TLFS	80	17	4	8	0	68
2013	IMVT, ROMO, SDOT, TLFS	119	26	7	19	6	87
2014	IMVT, ROMO, SDOT, TLFS	167	36	14	18	18	117
2015	TLFS	97	20	53	13	8	23
2016	TLFS	35	9	20	0	12	3
	Total	498	108	98	58	44	298
Lapland longspur							
Year	**Sites**	**Total**		**Un-hatched**	**Depredated**	**Non-predation death**	**Fledged**
		eggs	nests	eggs	eggs/ nestlings	nestlings	nestlings
2012	IMVT, ROMO, SDOT, TLFS	112	27	9	12	6	85
2013	IMVT, ROMO, SDOT, TLFS	132	27	25	23	15	69
2014	IMVT, ROMO, SDOT, TLFS	185	39	14	56	50	65
2015	TLFS	0	0	0	0	0	0
2016	TLFS	35	8	29	0	6	0
	Total	464	101	77	91	77	219

Table 3: A summary identifying the number of eggs and nests from re-nests or second broods each season at Imnavait (IMVT), Roche Moutonnee (ROMO), Sagavanirktok Department of Transportation (SDOT), and Toolik (TLFS) sites and the final fates of each. Un-hatched eggs include those that did not hatch due to lack of fertilization, unknown developmental defect, or abandonment. Depredated eggs include eggs or nestlings that were consumed (some eggs in this category may not have been fertilized). Non-predation deaths include all nestlings than died due to a factor other than predation (e.g. abandonment, illness, injury, hypothermia).

Gambel's white-crowned sparrow							
Year	**Sites**	**Total**		**Un-hatched**	**Depredated**	**Non-predation death**	**Fledged**
		eggs	nests	eggs	eggs/ nestlings	nestlings	nestlings
2012	IMVT, ROMO, SDOT, TLFS	7	2	0	4	0	3
2013	IMVT, ROMO, SDOT, TLFS	5	1	0	0	0	5
2014	IMVT, ROMO, SDOT, TLFS	11	3	0	0	5	6
2015	TLFS	56	14	2	17	9	28
2016	TLFS	40	10	7	2	8	23
	Total	119	30	9	23	22	65
Lapland longspur							
Year	**Sites**	**Total**		**Un-hatched**	**Depredated**	**Non-predation death**	**Fledged**
		eggs	nests	eggs	eggs/ nestlings	nestlings	nestlings
2012	IMVT, ROMO, SDOT, TLFS	0	0	0	0	0	0
2013	IMVT, ROMO, SDOT, TLFS	0	0	0	0	0	0
2014	IMVT, ROMO, SDOT, TLFS	5	1	0	5	0	0
2015	TLFS	0	0	0	0	0	0
2016	TLFS	0	0	0	0	0	0
	Total	5	1	0	5	0	0